Linear response in neuronal networks: from neurons dynamics to collective response

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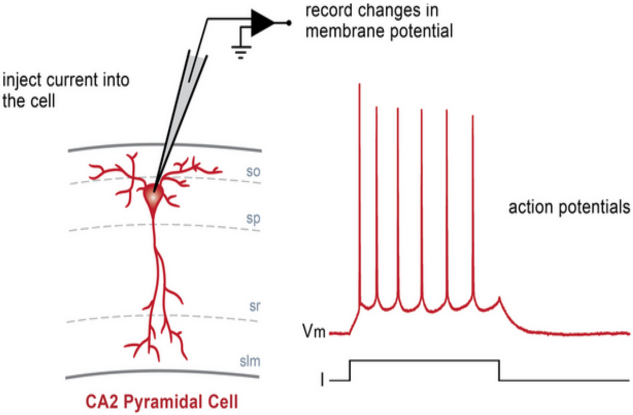
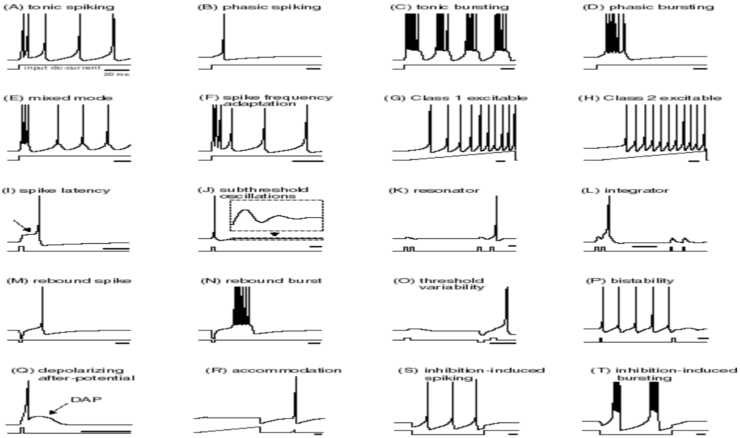
LACONEU summer school 2019.

Neuron response to a stimulus



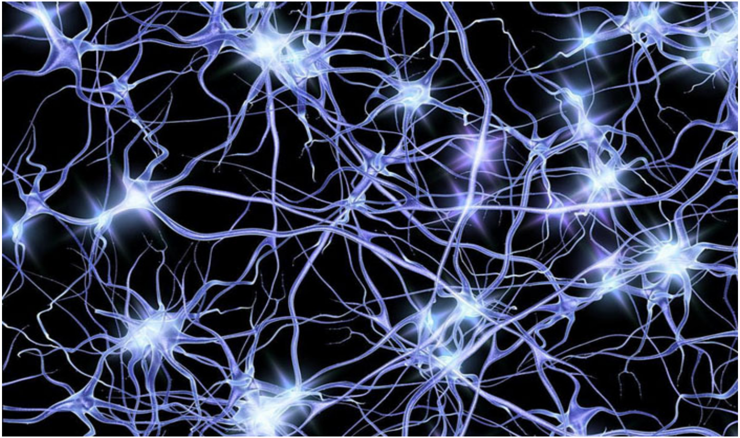
https://www.plasticitylab.com/methods/

Neuron response to a stimulus



Izhikevich, E., IEEE Trans Neural Netw , 15 (5), 10631070, (2004).

Network response to a stimulus



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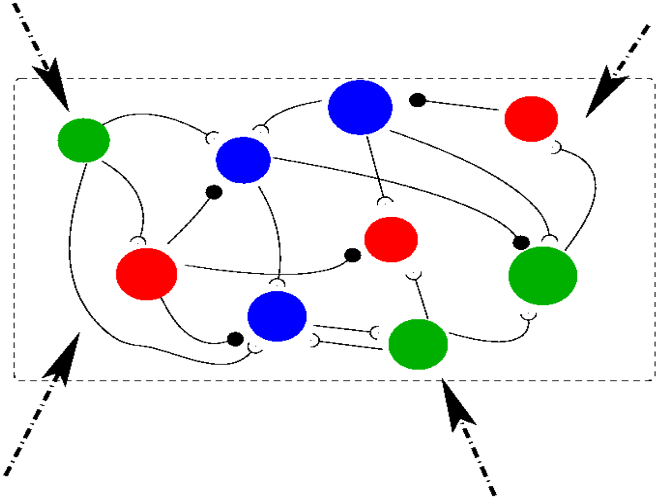

Network response to a stimulus

1. How does an input/ stimulation applied to a subgroup of neurons in a population affect the dynamics of the whole network ?

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1. How does an input/ stimulation applied to a subgroup of neurons in a population affect the dynamics of the whole network ?
2. How to measure the influence of a stimulated neuron on another neuron ?
3. How does this "effective connectivity" relates to :
   (a) Synaptic connectivity;
   (b) Pairwise correlations;
   (c) "Information" transport.

From firing rate neurons dynamics to linear response.

Amari-Wilson-Cowan model

Amari, 1971; Wilson-Cowan, 1972; Cohen-Grossberg, 1983; Sompolinsky et al, 1988; ...

$$\frac{dV_i}{dt} = -\mu V_i + \sum_{j=1}^{N} J_{ij} f(V_j(t)) + S_i(t); \quad i = 1 \dots N. \qquad (1)$$

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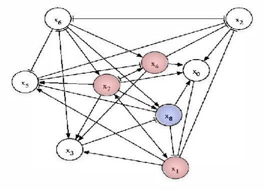
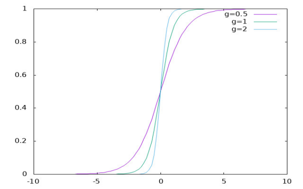


Ex: $J_{ij} \sim \mathcal{N}\left(0, \frac{J^2}{N}\right)$

(Sompolinsky et al, 1988)

Non linearity



Ex: $f(x) = \frac{1}{2}\left(1 + \tanh(gx)\right),$
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$$\frac{d\vec{V}}{dt} = -\mu \vec{V} + \mathcal{J}.f(\vec{V}) + \vec{S}(t); \quad i = 1 \dots N. \tag{1}$$

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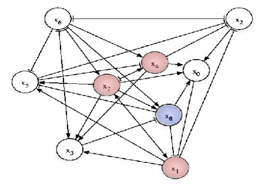

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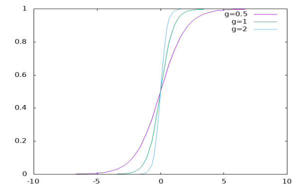

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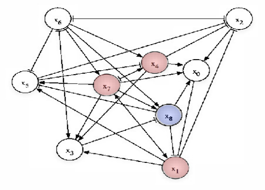

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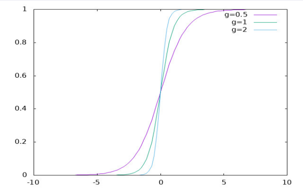

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Low gain g dynamics

Theorem. If g is small enough $\vec{G}$ is contractive.

$$\forall \vec{V}, \vec{V}' \in \mathcal{M}, \quad \|\vec{G}(\vec{V}') - \vec{G}(\vec{V})\| \leq \eta \|\vec{V}' - \vec{V}\|, \quad 0 < \eta < 1$$

$$\Rightarrow$$

For $\vec{S} = 0$, there is a unique stable fixed point $\vec{V}^*$, $\vec{G}(\vec{V}^*) = \vec{0}$.

Low gain g dynamics

Small perturbation of the fixed point. $\vec{V} = \vec{V}^* + \vec{\xi}.$

$$\frac{d\vec{\xi}}{dt} = DG_{\vec{V}^*}.\vec{\xi} + \vec{S}(t) + O\left(\|\vec{\xi}\|^2\right)$$

$$\vec{\xi}(t) = \int_{-\infty}^{t} e^{DG_{\vec{V}^*}(t-s)}.\vec{S}(s)ds$$

$$\Lambda = P^{-1}.DG_{\vec{V}^*}.P;\ \vec{\xi} = P\vec{\xi}';\ \vec{S} = P\vec{S}' \Rightarrow \vec{\xi}'(t) = \int_{-\infty}^{t} e^{\Lambda(t-s)}.\vec{S}'(s)ds$$

$$\xi_k'(t) = \int_{-\infty}^{t} e^{\lambda_k(t-s)}.S_k'(s)ds$$

Low gain g dynamics

Harmonic perturbation. $S'_k(t) = A'_k e^{i\omega t}$.

$$\lambda_k = \lambda_{k,r} + i\lambda_{k,i}; \quad \omega = \omega_r + i\omega_i.$$

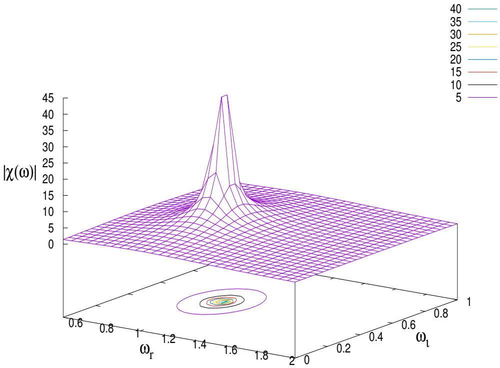
The integral is finite if $\omega_i < -\lambda_{k,r}$.

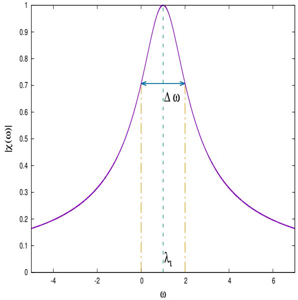
$$\xi'_k(t) = \hat{\chi}'_k(\omega) e^{i\omega t}.$$

Complex susceptibility matrix.

$$\vec{\xi}(t) = \hat{\chi}(\omega).\vec{S} e^{i\omega t}. \quad (2)$$

Low gain g dynamics





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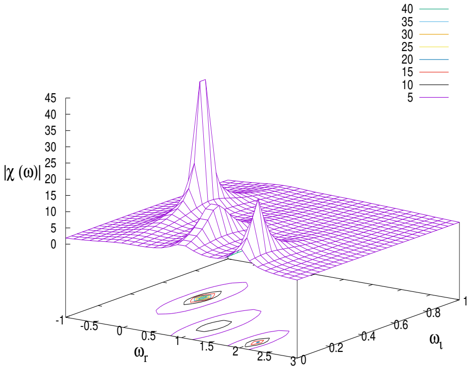

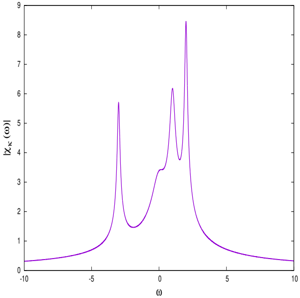

Low gain g dynamics

Example 1. $f(x) = \tanh(gx) \Rightarrow$

$$\vec{V}^* = \vec{0}; \quad DG_{\vec{V}^*} = -\mu\mathcal{I} + g\mathcal{J}$$

Let $s_k \equiv s_{k,r} + is_{k,i}$ eigenvalues of $\mathcal{J}$.

$$\lambda_k = \underbrace{-\mu + g\, s_{k,r}}_{\lambda_{k,r}} \pm i \underbrace{g\, s_{k,i}}_{\lambda_{k,i}}$$

When $\mathcal{J}$ is random, $J_{ij} \sim \mathcal{N}(0, \frac{J^2}{N})$ the probability distribution of eigenvalues is known.

(Girko, V. L., Theory Probab. Appl. 29, 694-706, 1984.).

Low gain g dynamics

Example 2. $f(x) = \frac{1+\tanh(gx)}{2} \Rightarrow$

$$\vec{V}^* \equiv \vec{V}^*(\mathcal{J}); \quad DG_{\vec{V}^*} = -\mu\mathcal{I} + gD(\vec{V}^*)\mathcal{J}$$

where $D(\vec{V}^*) = diag(\frac{1-\tanh^2(gV_i^*)}{2})$.

The eigenvalues of $D(\vec{V}^*)\mathcal{J}$ cannot be determined from the eigenvalues of $\mathcal{J}$. However, when $\mathcal{J}$ is random, $J_{ij} \sim \mathcal{N}(0, \frac{J^2}{N})$ the probability distribution of eigenvalues can be determined.

(Girko, V. L. Theory of Random Determinants. Boston, MA: Kluwer, 1990).

Low gain g dynamics

Summary:

- The linear response to a signal of weak amplitude is controlled by the Jacobian matrix $DG_{\vec{V}*}$.
- Eigenvalues of $DG_{\vec{V}*}$ $\Rightarrow$ Poles of the complex susceptibility $\Rightarrow$ Resonances.
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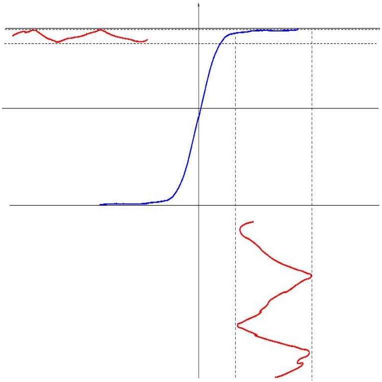
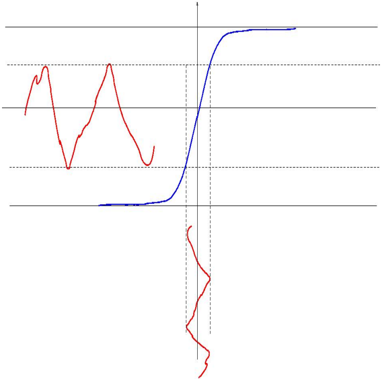
Expansion/Contraction

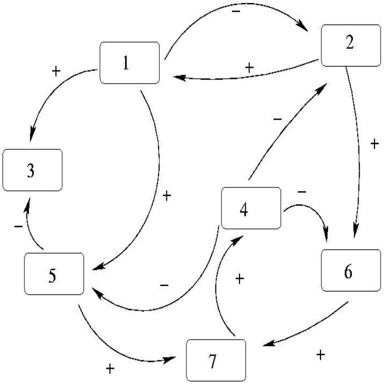


Saturation



Amplification

Expansion/Contraction



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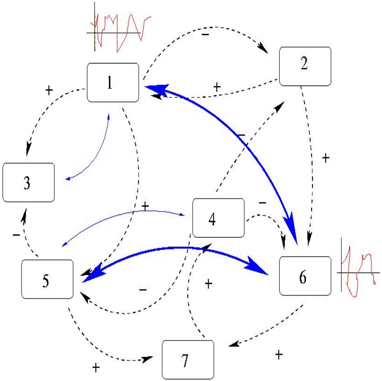

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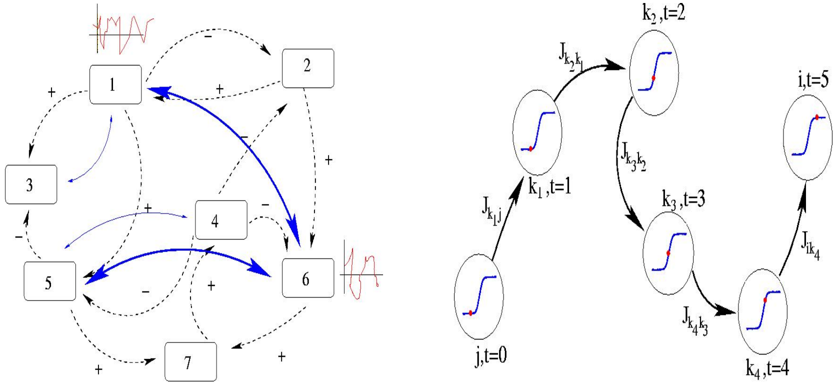

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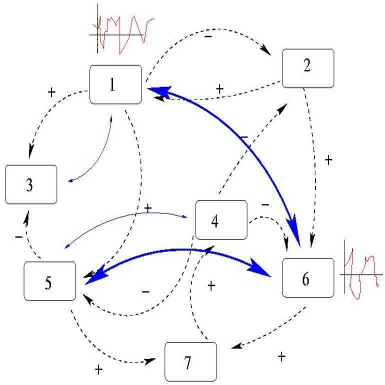
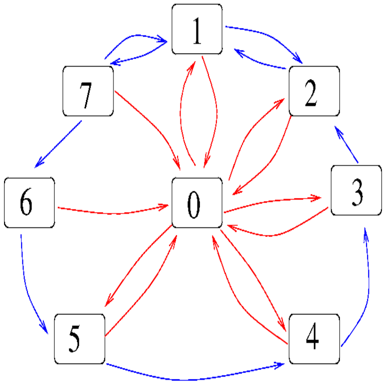




Linear response in a dynamical regime

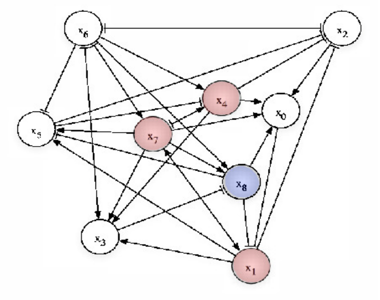
$$\frac{dV_i}{dt} = -\mu V_i + \sum_{j=1}^{N} J_{ij} f(V_j(t)) + I_i(t); \quad i = 1 \dots N.$$

$$V_i(t+dt) = V_i(t)(1-\mu dt) + \sum_{j=1}^{N} J_{ij} f(V_j(t)) dt + S_i(t) dt$$

$$V_i(t+1) = \sum_{j=1}^{N} J_{ij} f(V_j(t)) + S_i(t). \tag{3}$$

Linear response in the chaotic regime

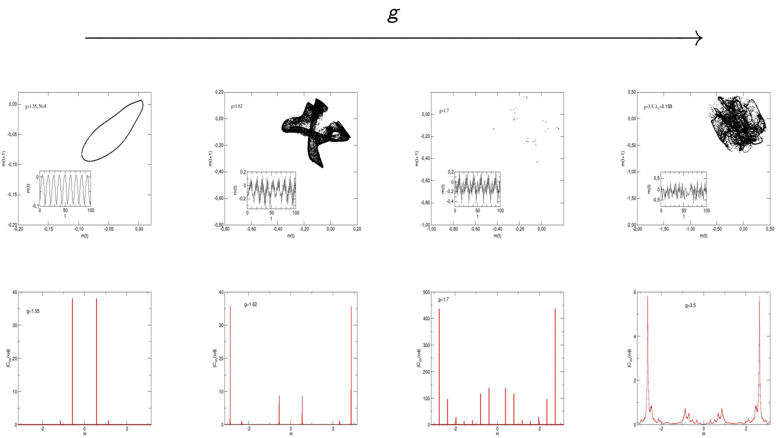
B. Cessac, J.A. Sepulchre, PRE (2004); Chaos (2006); Physica D (2006)



$$\vec{V}(t+1) = \underbrace{\mathcal{J}.f(\vec{V}(t))}_{\vec{G}(\vec{V}(t))} + \epsilon \vec{S}(t)$$

$$f(x) = \tanh(g\,x)$$

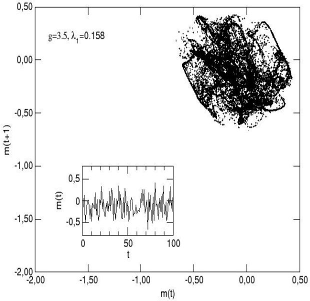
Transition to chaos by quasi periodity as g increases



Doyon B. et al, International Journal Of Bifurcation and Chaos, Vol. 3, Num. 2, 279-291 (1993)

Cessac B. et al, Physica D, 74, 24-44 (1994)

Chaotic dynamics and strange attractors



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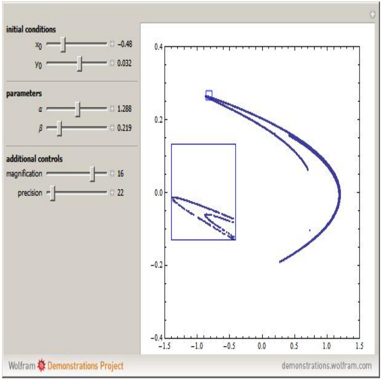


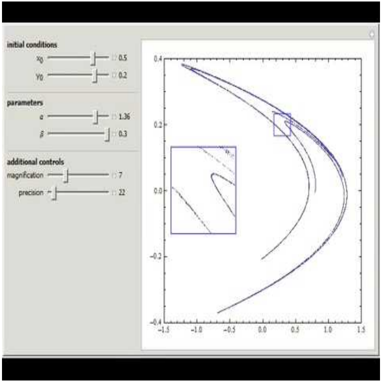
Hénon map

$$\begin{cases} x(t+1) & = 1 - ax^2(t) + y(t) \\ y(t+1) & = bx(t) \end{cases}$$

$$a = 1.4; b = 0.3$$

https://upload.wikimedia.org/wikipedia/commons/a/ac/

Chaotic dynamics and strange attractors



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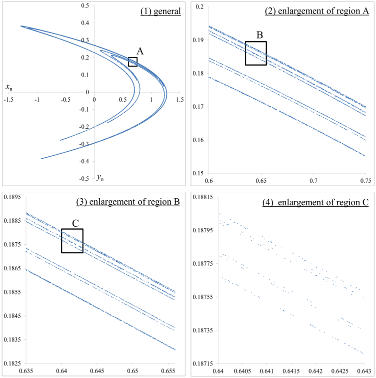

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http://www.demonstrations.wolfram.com/OrbitDiagramOfTheHenonMap/

Chaotic dynamics and strange attractors

Decomposition of Hénon's Transformation

The gridded square in the upper left is transformed in three steps: a nonlinear bending (upper right) in the y-direction, the contraction towards the y-axis (lower left) and a reflection at the diagonal (lower right). The region shown is $-2.2 \leq x \leq 2.2$ and $-2.2 \leq y \leq 2.2$.

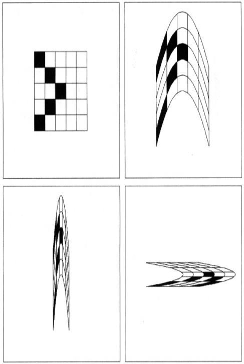

Figure 12.3

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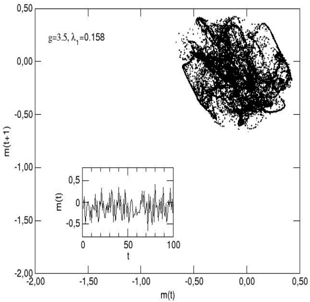
http://www.sfu.ca/ rpyke/335/W00/

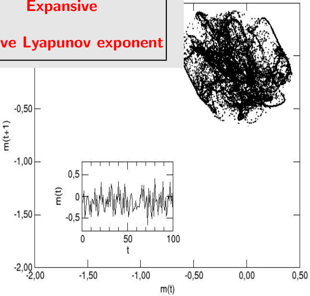
Chaotic dynamics and strange attractors

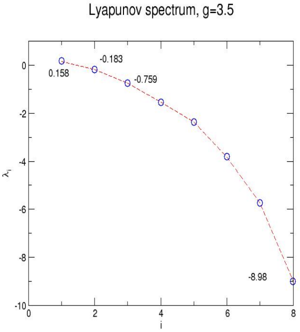


Chaotic dynamics and strange attractors

Expansive

Positive Lyapunov exponent





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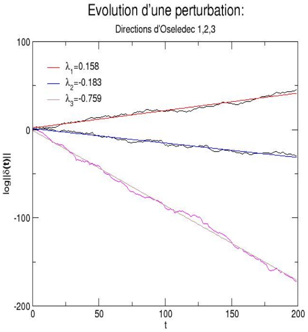

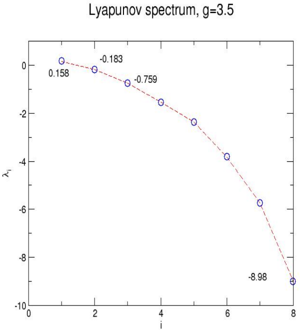

Time dependent perturbation

$$\vec{V}(t+1) = \vec{G}(\vec{V}(t)); \quad \vec{V}'(t+1) = \vec{G}(\vec{V}'(t)) + \epsilon\vec{S}(t)$$

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$$\vec{\delta}(t) = \vec{V}'(t) - \vec{V}(t) \Rightarrow \vec{\delta}(t_0+1) = \vec{V}'(t_0+1) - \vec{V}(t_0+1) = \epsilon \vec{S}(t_0)$$

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$$\vec{\delta}(t) = \epsilon\sum_{\tau=t_0}^{t-1} DG^{t-\tau+1}_{\vec{V}(t_0+1)}.\vec{S}(\tau) + \epsilon^2\vec{R}(t)$$

Time dependent perturbation

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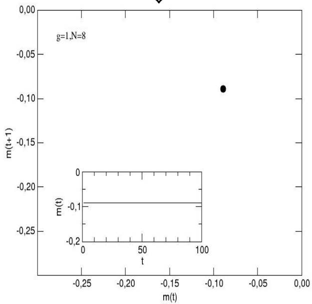

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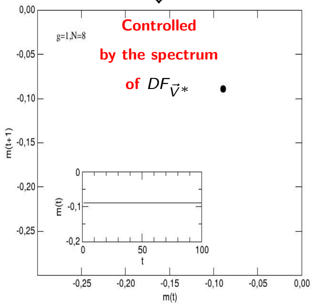

Linear stability analysis

$$\vec{G}(\vec{V}) = \mathcal{J} f(g\, \vec{V})$$

$$DF_{\vec{V}} = g \mathcal{J} \Lambda(\vec{V})$$

$$\Lambda_{ij} = f'(g\, u_j)\, \delta_{ij}$$

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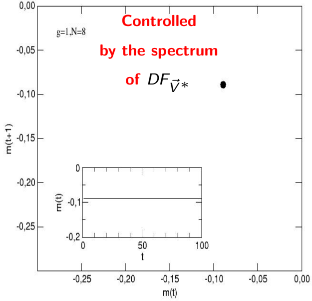
$$\vec{\delta}(t) = \epsilon \underbrace{\sum_{\tau=t_0}^{t-1} \left(DF_{\vec{V}} \right)^{t-\tau+1} .\vec{S}(\tau)}_{\text{Controlled by the spectrum of } DF_{\vec{V}*}} + \epsilon^2 \vec{R}(t)$$



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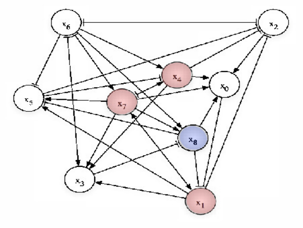

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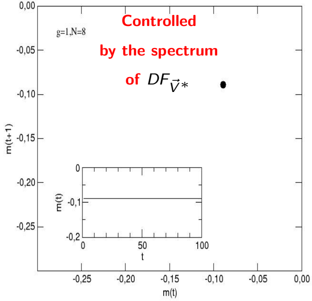

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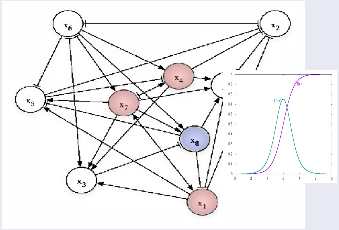
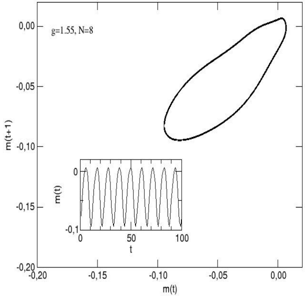


Time dependent perturbation

$$\vec{\delta}(t) = \epsilon \sum_{\tau=t_0}^{t-1} DF_{\vec{V}(t+1)}^{t-\tau+1} . \vec{S}(\tau) + \epsilon^2 \vec{R}(t)$$



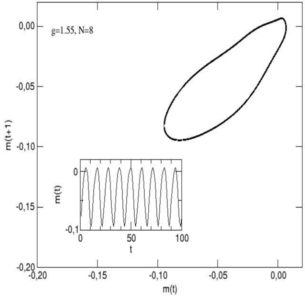
$$\vec{G}(\vec{V}) = \mathcal{J} f(g\,\vec{V}) + \theta$$

$$DF_{\vec{V}} = g\mathcal{J}\Lambda(\vec{V})$$

$$\Lambda_{ij} = f'(g\,u_j)\,\delta_{ij}$$

Time dependent perturbation

$$\vec{\delta}(t) = \epsilon \sum_{\tau=t_0}^{t-1} DF^{t-\tau+1}_{\vec{V}(t+1)}.\vec{S}(\tau) + \epsilon^2 \vec{R}(t)$$



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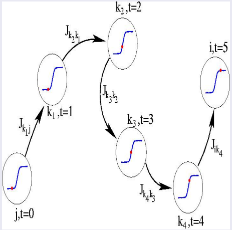

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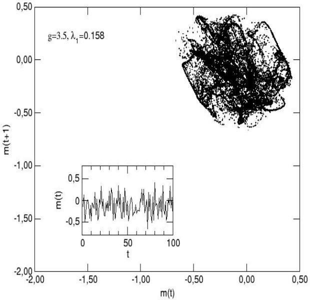

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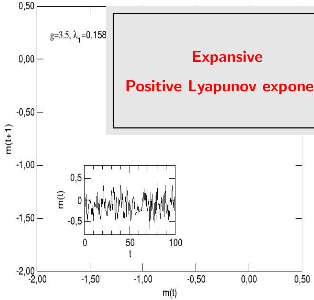
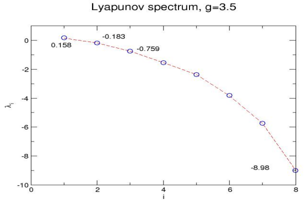
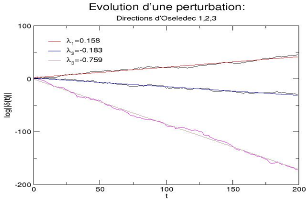


Expansive

Positive Lyapunov exponent





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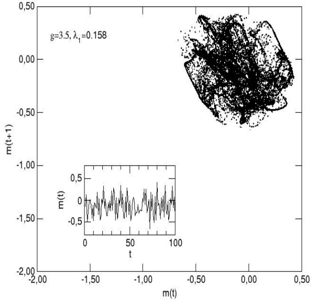

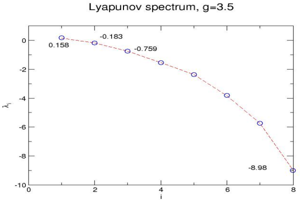

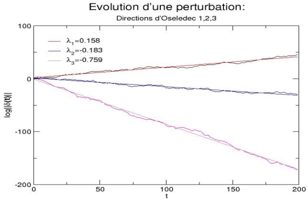

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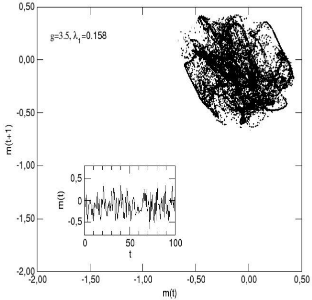


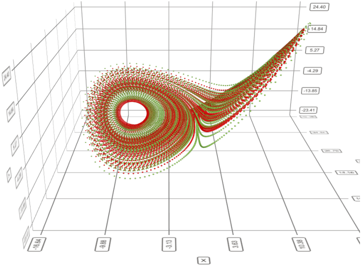
Linear response vs chaotic

Butterfly effect

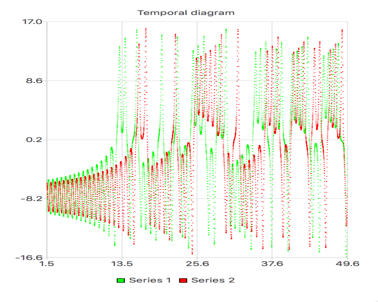
Van Kampen objection

The linear expansion provided by the positive Lyapunov exponent prevents linear response theory.

Time dependent perturbation



Linear response vs chaotic



The Sinai-Ruelle-Bowen measure

Time averaging is robust to perturbation.

$$\lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^{T} \Phi(\vec{G}^t(\vec{V})) = \lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^{T} \Phi(\vec{G}^t(\vec{V} + \vec{\delta}))$$

μ_L Lebesgue measure on the phase-space.

$$\mu \stackrel{w}{=} \lim_{t \to +\infty} \vec{G}^{*t} \mu_L, \quad \text{SRB measure}$$

$$\lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^{T} \Phi\left[\vec{G}^t(\vec{V})\right] \stackrel{\mu_L \, a.s.}{=} \int_{\Omega} \Phi(\vec{V}) \mu(d\mathbf{X})$$

Natural notion of averaging "on" the attractor.

The Sinai-Ruelle-Bowen measure

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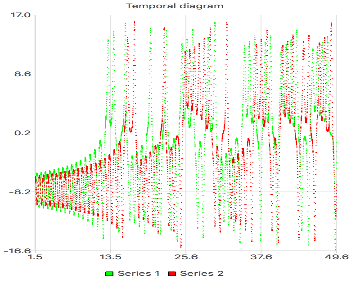

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Natural notion of averaging "on" the attractor.

Decomposition of Hénon's Transformation

The gridded square in the upper left is transformed in three steps: a non-linear bending (upper right) in the y-direction, the contraction towards the y-axis (lower left) and a reflection at the diagonal (lower right). The region shown is $-2.2 \leq x \leq 2.2$ and $-2.2 \leq y \leq 2.2$.

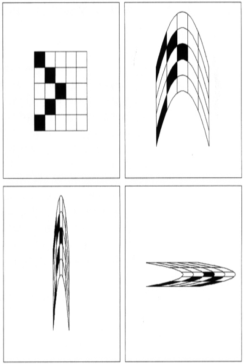

Figure 12.3

Out of equilibrium SRB state

D. Ruelle, J. Stat. Phys., 1998

$$\mu_t = \mu + \delta_t \mu = \lim_{n \to +\infty} \vec{G}'_t \dots \vec{G}'_{t-n} \mu$$

$$\delta_t \mu \left[\Phi\right] = \epsilon \sum_{\tau=-\infty}^{t-1} \int \mu(d\vec{V}) D\vec{G}_{\vec{V}}^{t-\tau-1} \vec{S}_\tau \left[\vec{G}^{-1}(\vec{V})\right] . \nabla_{\vec{V}(t-\tau-1)} \Phi + NL$$

$$\delta_t \mu[\Phi] = \epsilon \sum_{\sigma} \left\langle \kappa_\sigma \vec{S}_{t-\sigma-1} \circ \vec{G}^{-1} | \Phi \right\rangle_{\mathbf{eq}}$$

Linear response in the firing rate neural network

B. Cessac, J.A. Sepulchre, PRE (2004); Chaos (2006); Physica D (2006)

Convolution

$$\boxed{\delta_t \rho[u_i] = \epsilon \left[\chi * S \right]_i (t)}$$

$$= \epsilon \sum_{j=1}^{N} \sum_{\sigma=-\infty}^{t} \chi_{i,j}(\sigma) S_j(t-\sigma-1)$$

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$$\boxed{\chi_{i,j}(\sigma) = \sum_{\gamma_{ij}(\sigma)} \prod_{l=1}^{\sigma} J_{k_l k_{l-1}} \left\langle \prod_{l=1}^{\sigma} f'(u_{k_{l-1}}(l-1)) \right\rangle_{eq}}$$

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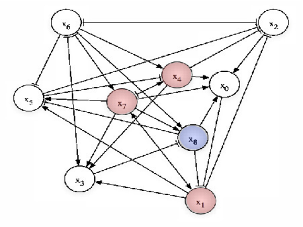

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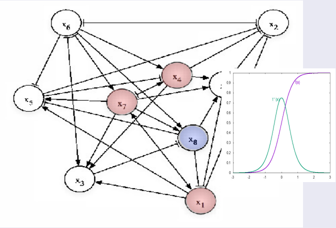

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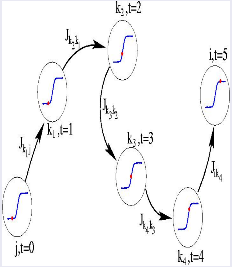

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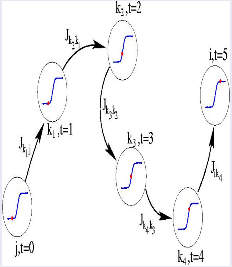

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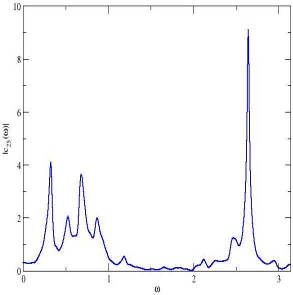
Resonances

Power spectrum

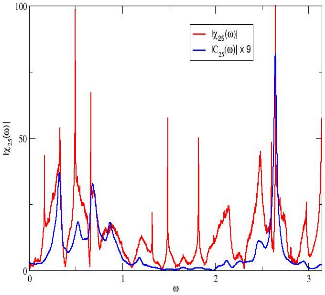


Ruelle resonances

- Ruelle-Pollicott resonances: In the power spectrum. Absolutely continuous part of the SRB measure.

Resonances

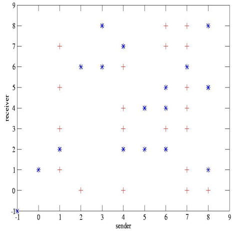
Complex susceptibility



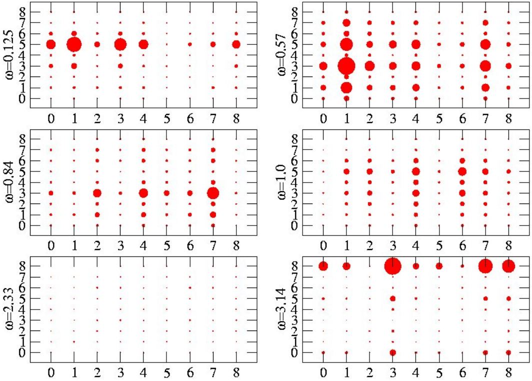
Ruelle resonances

- Ruelle-Pollicott resonances: In the power spectrum. Absolutely continuous part of the SRB measure.
- Exotic resonances. Not in the power spectrum. Singular part of the SRB measure.
- Predicted by D. Ruelle (J. Stat. Phys, 1999)
- Exhibited in B. Cessac, J.A. Sepulchre, PRE, 2004.

Response to a time-dependent stimulus

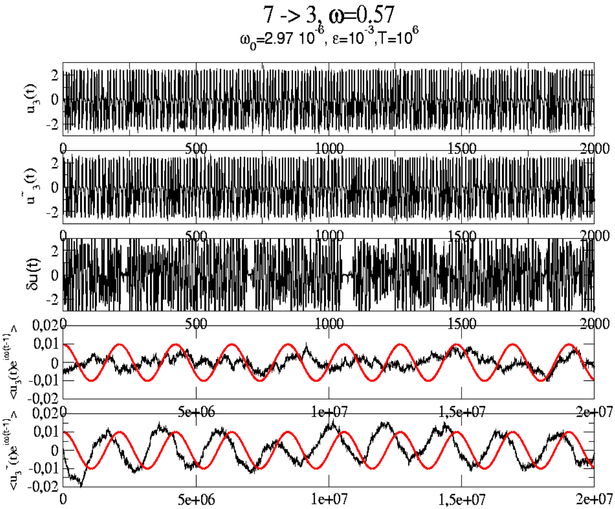


Connectivity matrix

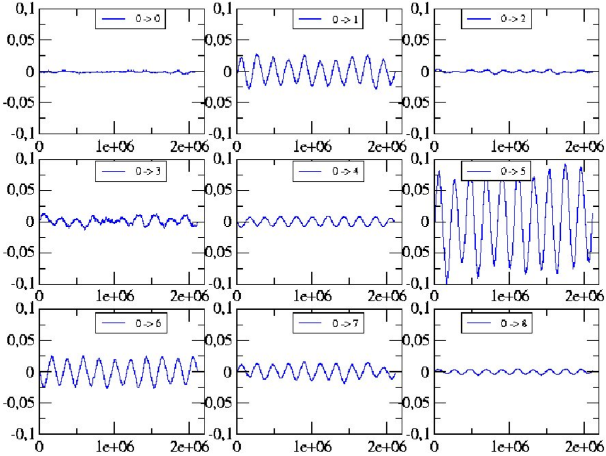


Response matrix

Response to a time-dependent stimulus

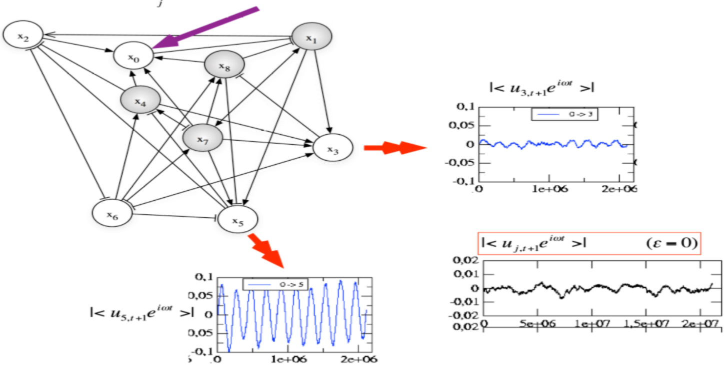


Response to a time-dependent stimulus



Response to a time-dependent stimulus

$$u_{0,t+1} = \sum_{j}^{N} J_{0j} f(u_{j,t}) + \varepsilon \cos(\omega_M t) \sin(\omega t) \qquad (\varepsilon \sim 10^{-3})$$



$$< u_{5,t+1} >= \varepsilon \chi_{50}(\omega) \cos(\omega_M t) \sin(\omega t + \phi_{50}(\omega)) + O(\varepsilon^2)$$

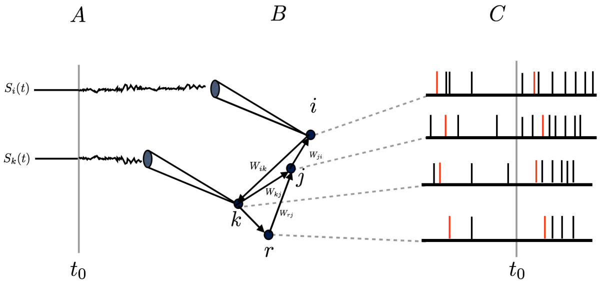
Main conclusions

- Linear response is possible in a chaotic neural network.
- Convolution kernel depending on synaptic graph and dynamics built on equilibrium (SRB) correlations.
- The response graph is different from the synaptic weights graph and depends on the stimulus.

From spiking neurons dynamics to linear response.

Linear response in spiking neuronal networks with unbounded memory

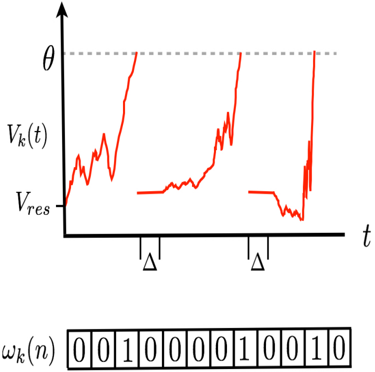
B. Cessac, R.Cofré, J. Math. Neuro. submitted, 2018



How are spike correlations modified by a time-dependent stimulus ?

An Integrate and Fire neural network model with chemical and electric synapses

R.Cofré, B. Cessac, Chaos, Solitons and Fractals, 2013



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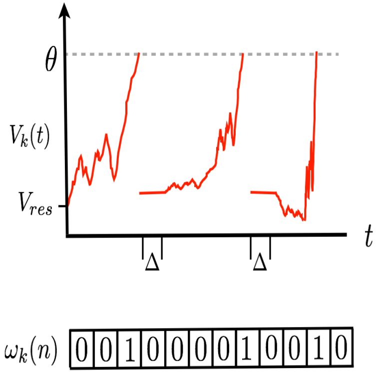


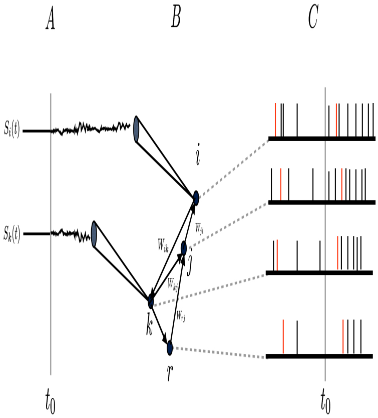
Spikes

- Voltage dynamics is time-continuous.
- Spikes are time-discrete events (time resolution $\delta > 0$).

$$t_k^{(l)} \in [n\delta, (n+1)\delta[$$
$$\Rightarrow$$
$$\omega_k(n) = 1$$

An Integrate and Fire neural network model with chemical and electric synapses

R.Cofré, B. Cessac, Chaos, Solitons and Fractals, 2013



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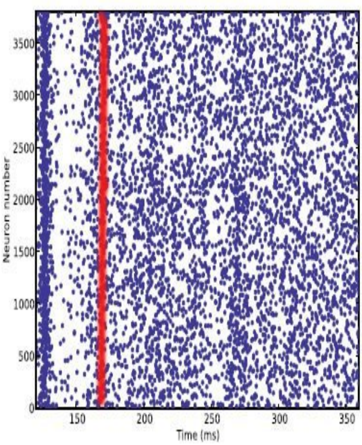
- Spike state $\omega_k(n) \in 0, 1$.

An Integrate and Fire neural network model with chemical and electric synapses

R.Cofré, B. Cessac, Chaos, Solitons and Fractals, 2013



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- Spike pattern $\omega(n)$.

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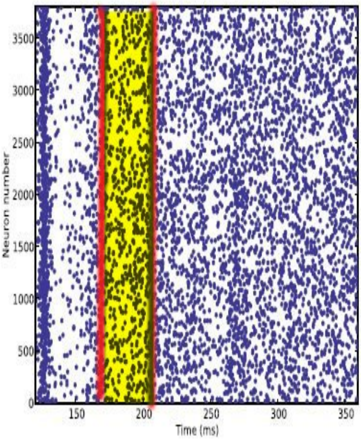
R.Cofré, B. Cessac, Chaos, Solitons and Fractals, 2013



Spikes

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- Spike state $\omega_k(n) \in 0, 1$.
- Spike pattern $\omega(n)$.
- Spike block ω_m^n.

A conductance-based Integrate and Fire model

M. Rudolph, A. Destexhe, Neural Comput. 2006, (GIF model)

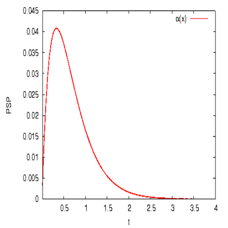
R.Cofré, B. Cessac, Chaos, Solitons and Fractals, 2013

Sub-threshold dynamics:

$$C_k \frac{dV_k}{dt} = -g_{L,k}(V_k - E_L)$$

$$-\sum_j g_{kj}(t,\omega)(V_k - E_j)$$

Synapses



$$\alpha_{kj}(t) = \frac{t}{\tau} e^{-\frac{t}{\tau_{kj}}} H(t),$$

A conductance-based Integrate and Fire model

M. Rudolph, A. Destexhe, Neural Comput. 2006, (GIF model)

R.Cofré, B. Cessac, Chaos, Solitons and Fractals, 2013

Sub-threshold dynamics:

$$C_k \frac{dV_k}{dt} = -g_{L,k}(V_k - E_L)$$

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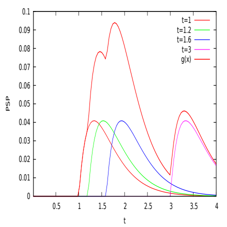

$$g_{kj}(t) = g_{kj}(t_j) + G_{kj}\alpha_{kj}(t - t_j)$$

$$t > t_j$$

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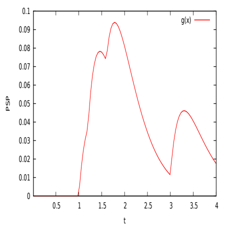

$$g_{kj}(t) = G_{kj} \sum_{n \geq 0} \alpha_{kj}(t - t_j^{(n)})$$

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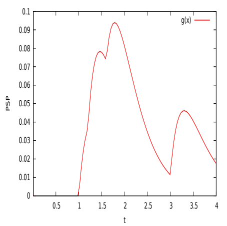

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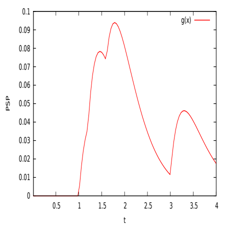

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A conductance-based Integrate and Fire model

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$$W_{kj} \stackrel{\text{def}}{=} G_{kj} E_j$$

$$\alpha_{kj}(t,\omega) = \sum_{n\geq 0} \alpha_{kj}(t-n\delta)\omega_j(n)$$

$$i_k(t,\omega) = g_{L,k}E_L + \sum_j W_{kj}\alpha_{kj}(t,\omega) + S_k(t) + \sigma_B \xi_k(t)$$

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$$\Gamma_k(t_1, t, \omega) = e^{-\frac{1}{C_k}\int_{t_1 \vee \tau_k(t,\omega)}^{t} g_k(\,u,\omega\,)\,du}$$

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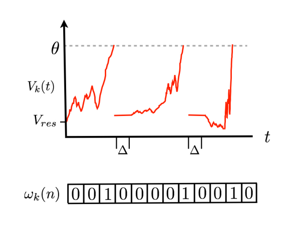

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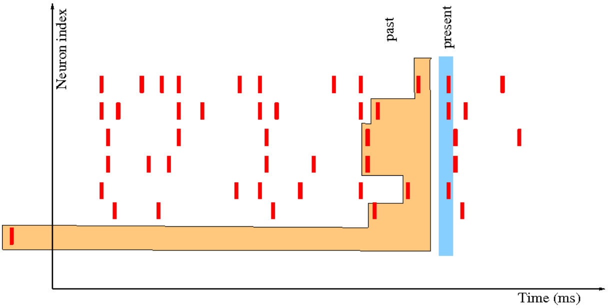
A conductance-based Integrate and Fire model

Variable length Markov chain

$$P_n\left[\omega(n) \,\middle|\, \omega_{-\infty}^{n-1}\right] \equiv \Pi\left(\omega(n), \frac{V_{th} - V_k^{(det)}(n-1,\omega)}{\sigma_k(n-1,\omega)}\right)$$



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History dependence.

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History dependence, observable, network dynamics

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History dependence, (spontaneous) correlation between observable and network dynamics

Response to stimuli in a mean-field limit

Characteristic time

$$\tau_{d,k} = \frac{C_k}{g_L + \sum_{j=1}^{N} G_{kj}\nu_j\tau_{kj}}$$

Approximations

(i) Replace $\tau_k(r-1,.)$ by $-\infty$;

(ii) Replace $\Gamma_k(t_1, r-1, \omega) = e^{-\frac{1}{C_k}\int_{t_1}^{r-1} g_k(\,u,\omega\,)\,du}$ by $e^{-\frac{(r-1-t_1)}{\tau_{d,k}}}$.

Response to stimuli in a mean-field limit

$$\delta^{(1)}\mu\,[\,f(t)\,] =$$

$$-\frac{2}{\sigma_B}\sum_{k=1}^{N}\frac{1}{\sqrt{\tau_{d,k}}}\sum_{r=-\infty}^{n=[\,t\,]}\left[\qquad\qquad\right](\,S_k * e_{d,k}\,)(r-1)$$

$$e_{d,k}(u) = e^{-\frac{u}{\tau_{d,k}}}$$

Response to stimuli in a mean-field limit

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Markov approximation with memory depth 1

$$\left[\begin{array}{ll} & \gamma_k^{(1)}\,\mathcal{C}^{(sp)}\left[\,f(t,\cdot),\omega_k(r)\,\right] \\ +\sum_{i=1}^{N} & \gamma_{k;i}^{(2)}\,\mathcal{C}^{(sp)}\left[\,f(t,\cdot),\omega_k(r)\,\omega_i(r-1)\,\right] \\ +\sum_{i,j=1}^{N} & \gamma_{k;ij}^{(3)}\,\mathcal{C}^{(sp)}\left[\,f(t,\cdot),\omega_k(r)\,\omega_i(r-1)\,\omega_j(r-1)\,\right] \\ + & \cdots \end{array}\right]$$

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Response to stimuli in a mean-field limit

Ex: Firing rate of neuron m

$$\delta^{(1)}\mu\left[\,\omega_m(t)\,\right] =$$

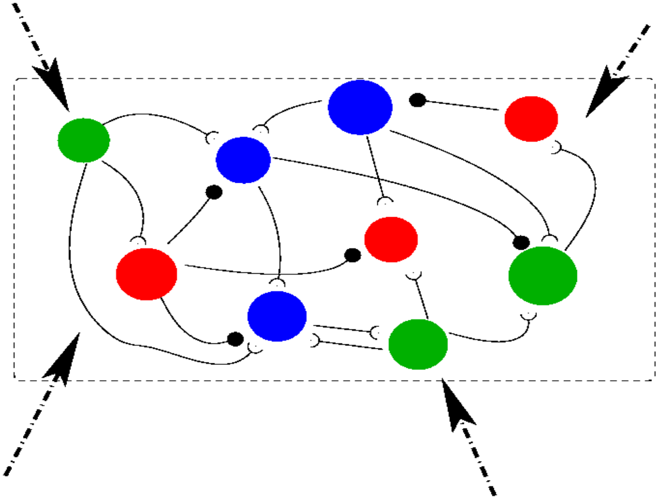
$$-\frac{2}{\sigma_B}\sum_{k=1}^{N}\frac{1}{\sqrt{\tau_{d,k}}}\sum_{r=-\infty}^{n=[\,t\,]}\left[\begin{array}{ll} & \gamma_k^{(1)}\,\mathcal{C}^{(sp)}\left[\,\omega_m(t),\,\omega_k(r)\,\right] \\ +\sum_{i=1}^{N} & \gamma_{k;i}^{(2)}\,\mathcal{C}^{(sp)}\left[\,\omega_m(t),\,\omega_k(r)\,\omega_i(r-1)\,\right] \\ +\sum_{i,j=1}^{N} & \gamma_{k;ij}^{(3)}\,\mathcal{C}^{(sp)}\left[\,\omega_m(t),\,\omega_k(r)\,\omega_i(r-1)\,\omega_j(r-1)\,\right] \\ + & \cdots \end{array}\right]\left(S_k * e_{d,k}\right)(r-1)$$

Conclusions

- Linear response in a spiking neural network.
- Convolution kernel depending on synaptic graph and dynamics built on equilibrium correlations.
- Link with receptive fields for sensory neurons ?
- Further steps. Handle this equation ... in a simple numerical example.

General conclusions

Network response to a stimulus



Network response to a stimulus

1. How does an input/ stimulation applied to a subgroup of neurons in a population affect the dynamics of the whole network ?
2. How to measure the influence of a stimulated neuron on another neuron ?
3. How does this "effective connectivity" relates to :
   (a) Synaptic connectivity;
   (b) Pairwise correlations;
   (c) "Information" transport.

Network response to a stimulus

Spontaneous dynamics $\Rightarrow$ complex, noise, chaos, non linear.

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Information transport ? Requires a suitable probabilitic characterization (entropy transport, Granger causality, ...).

Linear response theory in physics

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- Equilibrium stat. phys. (Max. Entropy Principle).

$$P[S] = \frac{1}{Z} e^{-\beta H\{S\}}$$

$$H\{S\} = \sum_\alpha \lambda_\alpha X_\alpha \{S\}$$

$$\lambda_\alpha X_\alpha \sim E, P \times V, \mu \times N, h \times M, \ldots$$

$$PV = nRT, \ldots$$

Linear response theory in physics

- Equilibrium stat. phys. (Max. Entropy Principle).
- Non equilibrium stat. phys. Onsager theory.

$$\vec{j}_\alpha = \vec{\mathcal{F}}_\alpha(\vec{\nabla}\lambda_1, \dots, \vec{\nabla}\lambda_\beta, \dots)$$

$$\vec{j}_\alpha \sim \sum_\beta L_{\alpha\beta} \vec{\nabla}\lambda_\beta + \dots$$

$$\vec{j}_{el} = -\sigma_E \vec{\nabla} V; \quad \vec{j}_Q = -\lambda \vec{\nabla} T, \dots$$

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Linear transport coefficients

$\leftarrow$

equilibrium correlations of currents.

Linear response theory in physics

Onsager theory in non equilibrium statistical mechanics.

gradients $\Rightarrow$ fluxes

Linear relation between "small" gradients and fluxes.

Linear response theory in physics

Onsager-Ruelle - . . . theory in dynamical systems.

Perturbation $\Rightarrow$ response

Linear relation between "small" perturbations and response.

Gibbs distribution

- Equilibrium stat. phys. (Max. Entropy Principle).
- Non equ. stat. phys. Onsager theory.
- Ergodic theory, chaotic systems.

The Sinai-Ruelle-Bowen measure is a Gibbs measure

$$H = -\log \det \Pi^u DF_X$$

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- Markov chains - finite memory.

$$P[\omega] = \frac{1}{Z} e^{-\beta H(\omega)}$$

$$H(\omega) = \sum_\alpha \lambda_\alpha X_\alpha(\omega)$$

$$X_\alpha(\omega) = \text{Product of spike events}$$

Hammersley, Clifford, unpublished, 1971

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- Markov chains - finite memory.
- Chains with complete connections - infinite memory (Left Interval Specification).

$$P\,[\,\omega\,] = \frac{1}{Z} e^{-\beta H(\,\omega\,)}$$

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Hammersley, Clifford, unpublished, 1971

O. Onicescu and G. Mihoc. CRAS Paris, 1935

R. Fernandez, G. Maillard, A. Le Ny, J.R. Chazottes, ...

Thanks !!